Research Article Journal of Orthoptera Research 2026, 35(1): 41–48

To fly or to jump: Factors related to the mode of locomotion for escape by the Japanese rice grasshopper *Oxya yezoensis*

Tatsuru Kuga[1,2], Eiiti Kasuya[3,4]

1 Graduate School of Systems Life Sciences, Kyusyu University, 744 Motooka, Nishi-ku, Fukuoka 819-0395, Japan.
2 Present address: Hiroshima City Insectarium, 10173 Aza-Fujigamaru, Fukuda-cho, Higashi-ku, Hiroshima 732-0036, Japan.
3 Department of Biology, Kyushu University, 744 Motooka, Nishi-ku, Fukuoka 819-0395, Japan.
4 Present address: Graduate School of Science, Osaka Metropolitan University, Gakuen, Naka-ku, Sakai, Osaka 599-8531, Japan.

Corresponding author: Tatsuru Kuga (tkuga486@gmail.com)

Academic editor: Diptarup Nandi | Received 11 January 2025 | Accepted 12 May 2025 | Published 22 January 2026

https://zoobank.org/55F4BA49-6FBB-4F2C-BE4C-7DE18520B0B1

Citation: Kuga T, Kasuya E (2026) To fly or to jump: Factors related to the mode of locomotion for escape by the Japanese rice grasshopper *Oxya yezoensis*. Journal of Orthoptera Research 35(1): 41–48. https://doi.org/10.3897/jor.35.146467

Abstract

Various grasshopper species exhibit two modes of locomotion—flying and jumping—when escaping approaching predators. A field experiment on the Japanese rice grasshopper *Oxya yezoensis* was conducted to identify factors related to the decision of locomotion mode during escape attempt. A human investigator, acting as a predator model, approached each grasshopper three times consecutively. The relationship between locomotion mode and the following factors was examined: grass height, air temperature, and relative humidity as environmental factors; sex, body length, body weight, and wing length as prey traits; persistence in approaches as a predator trait; and flight initiation distance (the distance between predator and prey when the escape behavior is triggered) and distance fled (the distance moved by the prey during escape) as additional escape strategies. The results showed that females escaped by jumping more frequently than males. Moreover, the distances fled by grasshoppers escaping by flying were greater than those of grasshoppers escaping by jumping. Flight initiation distances of grasshoppers that jumped were either shorter than or comparable to those that flew. In the first escape attempt, escape by flying increased with wing length in females, increased with air temperature, and decreased with relative humidity in both sexes. In repeated escape attempts, grasshoppers consistently used the same locomotion mode more frequently than expected if decisions of locomotion modes were made independently. These results indicate that *O. yezoensis* uses two modes of locomotion depending on various ecological and biological factors in the field.

Keywords

Antipredator tactics, distance fled, flight initiation distance, predator–prey interaction

Introduction

When approached by predators, prey animals escape utilizing various modes of locomotion, such as walking, running, hopping, flying, jumping, and swimming (Miller et al. 2011, Lee et al. 2013, Bateman and Fleming 2015). The diversity in locomotion modes during escape attempts is a consequence of evolution under predation pressures. This variation occurs not only between species but also within species (Dangles et al. 2007, Rodriguez-Prieto et al. 2008, de Barros et al. 2010, Miller et al. 2011). When a prey species can employ multiple locomotion modes, how does it decide which mode to use for escape? This question remains unexplored in many prey animals. Most studies on escape behaviors have focused on the predator–prey distance at the start of escape, termed flight initiation distance (FID), or the distance moved by the prey during escape, termed distance fled (DF) (Cooper and Blumstein 2015). In contrast, research on locomotion modes during escape remains limited (Miller et al. 2011). Different locomotion modes provide differences in movable distances, energetic cost, speed and/or trajectory (Rodriguez-Prieto et al. 2008, Miller et al. 2011). Thus, for survival, prey should use appropriate locomotion modes depending on the situation.

Grasshoppers are frequently used in studies of escape behavior (Lagos 2017). Various grasshoppers use at least two modes of locomotion during escape: flying and jumping (Forsman 1999, Butler 2013, Maeno et al. 2019, Kuga and Kasuya 2024). Flying allows long-distance escape (Forsman 1999), whereas jumping allows movement without additional energy consumption caused by wing flapping. Air temperature has been reported to affect the decision of locomotion mode during escape (Forsman 1999, Maeno et al. 2019). However, factors other than air temperature that might affect this decision have not been sufficiently studied despite being crucial for understanding grasshoppers' escape behaviors.

We hypothesized that grasshoppers use different locomotion modes depending on environmental factors, their traits, and the predator's traits. As a prey model that escapes by flying or jumping in the field, the Japanese rice grasshopper *Oxya yezoensis* Shiraki, 1910 was used in this study. We examined several factors for their potential relationship to locomotion modes: grass

Copyright *Tatsuru Kuga & Eiiti Kasuya*. This is an open access article distributed under the terms of the Creative Commons Attribution License (CC BY 4.0), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

height, air temperature, and relative humidity as environmental factors; sex, body length, body weight, and wing length as prey traits; and persistence in approach as a predator trait. High grass may hinder the movement of grasshoppers (Hochkirch et al. 2002) and thus hinder wing opening for flight after taking off. As in previous studies, high air temperature is predicted to increase flying (Forsman 1999, Maeno et al. 2019). High humidity decreases wing-beat frequencies of some insects (Parmezan et al. 2021; see also Belton 1986), thus is predicted to decrease the use of flying in *O. yezoensis*. Females are predicted to escape by jumping more frequently than males because of the trade-off between flight capability and reproduction (Chang et al. 2021). Individuals with short wings and/or heavy weights are predicted to prefer jumping because of their high wing-loading. In addition, large *O. yezoensis* is predicted to prefer flying because large insects are considered to be at high predation risk (Whitman and Vincent 2008). Persistent pursuit indicates high predation risk (Bateman and Fleming 2014) and is predicted to increase the use of flying for long-distance escape.

We also explored the relationships among FIDs, DFs, and the locomotion modes of *O. yezoensis*. An energetically expensive but high-performance mode of locomotion is preferred when the escape is delayed, and thus, FID is short (Rodriguez-Prieto et al. 2008). The short FID is predicted to increase the use of flying by *O. yezoensis*. Flying allows orthopteran insects to escape further (Forsman 1999); therefore, it is expected to result in long DF in *O. yezoensis*.

Materials and methods

Study sites.—Field experiments were conducted with adult *O. yezoensis* (Fig. 1A) in the Biodiversity Conservation Zone of Kyushu University, Fukuoka, Japan (33°35'46.1"N, 130°12'49.9"E). Seven grassland sites within the Biodiversity Conservation Zone were designated for the experiments. The grass height at six of the seven sites was lower than that at the remaining site. We classified the six sites with a mean grass height of 30 cm or less as low-grass sites (Fig. 1B; area, 120–540 m^2) and the remaining site, where the mean grass height exceeded 30 cm, as a high-grass site (Fig. 1C; area, 432 m^2). Because the low-grass sites contained bare patches, grass density was lower than in the high-grass site. However, this did not change our prediction regarding differences between high- and low-grass sites: Long and dense grasses would interfere with wing opening after taking off and increase the use of jumping, whereas short and sparse grasses would make it easy for predators to track grasshoppers and increase the use of flying for long-distance escape. All sites contained similar plant and animal species, and *O. yezoensis* was able to move between them.

Experimental procedure.—Human investigators have frequently been used as predator models to elicit escape behaviors in various grasshopper species (Cooper 2006, Butler 2013, Bateman and Fleming 2014, Collier and Hodgson 2017, Maeno et al. 2019). This approach is particularly relevant to *O. yezoensis*, as Japanese people have historically captured this species for food and recreation, although such customs are declining (Nonaka 2009, Mitsuhashi 2012). Therefore, one of the authors (TK) acted as a predator model by approaching the grasshoppers. During the approach, he carried two cameras on his waist to record the escape behavior of *O. yezoensis*: a high-speed digital camera (Casio EX-ZR1700; 120 frames per second) and a conventional digital camera (Sony DSC-WX170; 60 interlaced fields per second). To minimize the influence of the predator's appearance on the results, TK maintained a consistent appearance by wearing identical clothing and gear throughout the experiment.

Field experiments were conducted between October 6 and November 17, 2016, exclusively on rain-free days. At each site, TK approached a grasshopper three times consecutively before moving to another site to repeat the procedure. This process was conducted between 9:00 and 16:00 each day. High-grass and low-grass sites were selected at a ratio of 1:2. To minimize disturbance to the grasshoppers, a minimum of 40 min was allowed to elapse before revisiting a previously used site in the experiment.

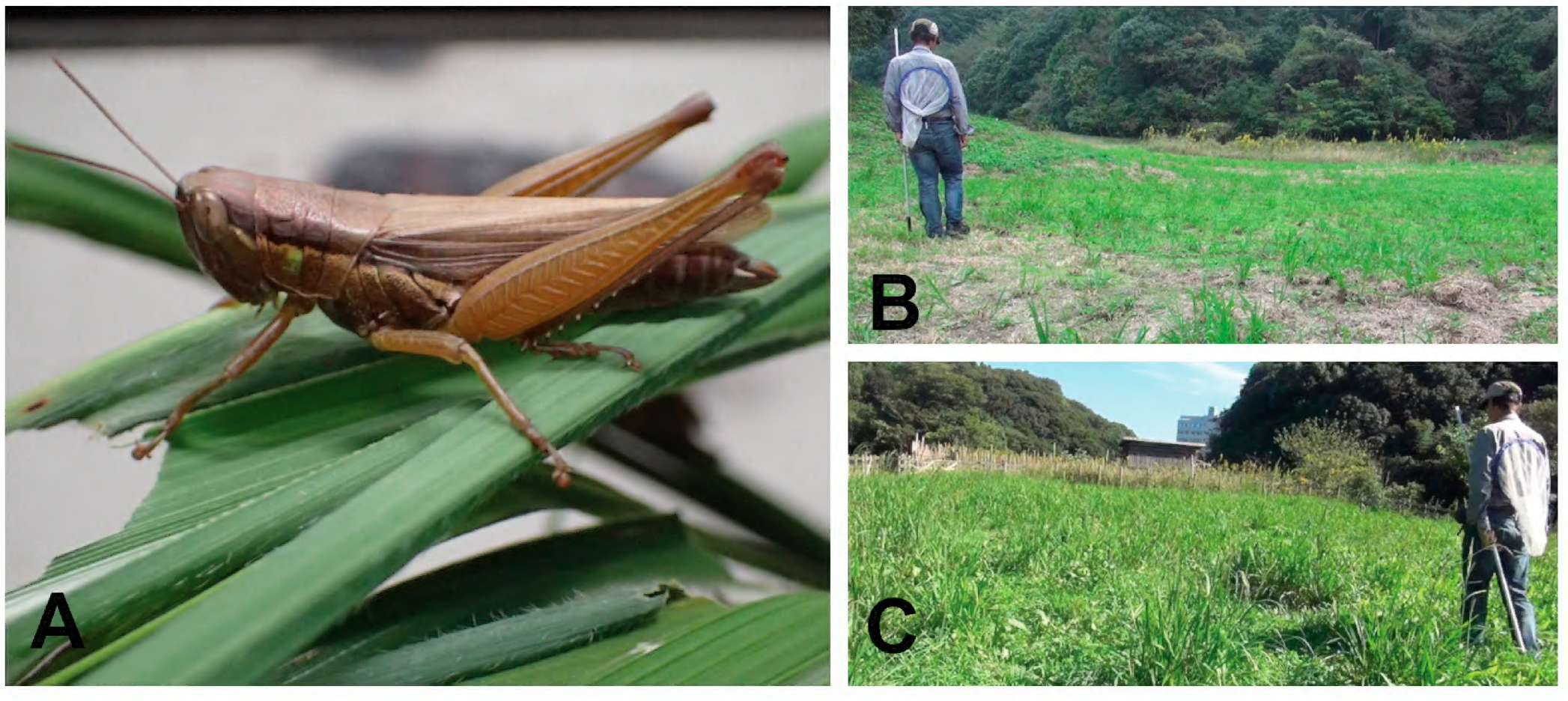

Fig. 1. Photos of *Oxya yezoensis* and experimental locations. **A.** Lateral view of a female; **B.** Low-grass site; **C.** High-grass site. A human investigator serving as a predator model is visible in the grassland photos.

Following the method of Kuga and Kasuya (2024), data collection for each individual involved a three-step procedure: identification of a target grasshopper, three consecutive approaches, and capture. The investigator searched for *O. yezoensis* by walking through a site at a pace of one step per second (1.01 ± 0.03 steps/sec, approximately 20 m/min; $n = 10$) guided by the sound of an electronic metronome (KORG TM-50; BPM = 60). Each area within a site was searched only once during each experimental procedure. Grasshoppers missing a hind leg due to autotomy were excluded from the study. Upon locating a target grasshopper, TK performed three consecutive approaches. Each approach was terminated immediately when the target initiated escape behavior. At this point, two wire ring markers (radius 8.5 cm) were placed at the locations of the investigator and the grasshopper. Subsequent approaches to the same target commenced shortly after marker placement. Following the third escape, TK captured the grasshopper and marked its final stopping point.

Data collection was terminated if the investigator lost sight of the target grasshopper during the approach or capture phase. In such cases, the investigator reinitiated the identification step to locate another target within the same site. To ensure balanced sample sizes between sexes, the identification step was also reinitiated if data had been collected from three consecutive grasshoppers of the same sex and another individual of the same sex was encountered. This sex-dependent restart was not implemented after mid-November or if more than half of the site area had been searched, due to the increasing difficulty in locating new targets at these times. If the three approaches and capture of a single target could not be successfully completed after searching the entire area of the site, the experiment at that site was concluded, and a new experiment was initiated at a different site.

Measurements.—The locomotion mode of *O. yezoensis* during escape was classified based on video footage recorded by the two cameras mounted on TK. An escape involving wing flapping was classified as flying, whereas an escape without wing flapping was classified as jumping. Target grasshoppers often escaped out of the camera frame, and in such cases, the locomotion mode outside the camera frame was confirmed directly by the investigator as the subject was approached. If wing flapping was not captured in the video but observed by the investigator, the locomotion mode was classified as flying.

FID, DF, ambient temperature, and relative humidity were recorded after each capture at the respective sites. FID and DF were measured to the nearest 1 cm using a steel tape measure. FID was defined as the distance between markers placed at the positions of the target grasshopper and TK at the initiation of each escape attempt. DF was defined as the distance between the markers placed at the target grasshopper's positions at the initiation and end of each escape attempt. Repeated approaches started after short intervals; therefore, the markers placed at the starting points of the second and third escapes were treated as the endpoints of the first and second escapes, respectively. Ambient temperature (to the nearest 1°C) and relative humidity (to the nearest 1%) were measured using a digital thermo-hygrometer (BIGMAN BM-7601).

The morphological traits of *O. yezoensis* were recorded daily after the last experiment. Body weight was measured to the nearest 0.01 g using an electronic scale (Sartorius 1416MP8). Body length, defined as the distance from the tip of the head to the end of the abdomen, and wing length, defined as the distance from the posterior end of the pronotum to the end of the forewings, were measured to the nearest 0.01 mm using a dial caliper (TAJIMA DIAL-15). All individuals were marked on their pronotum using a marker pen (Magic M551) and released into the field. They were not used as experimental targets in subsequent trials to avoid resampling of the same individual.

Statistical analyses.—We examined the relationship between locomotion mode and sex, FID, and DF for each of the three consecutive escape attempts. Sex differences in the proportions of flying and jumping were tested using Fisher's exact test. Differences in FIDs and DFs between individuals that escaped by jumping and flying were analyzed using the Brunner–Munzel test. These tests were performed separately for data collected from the low- and high-grass sites.

The relationships among environmental factors, prey traits, and locomotion modes were analyzed using a generalized linear model (GLM) with a quasi-binomial error structure and a logit link. The model fit both male and female data. The objective variable was the mode of locomotion during the first escape (fly = 0, jump = 1). Data from the second and third escapes were excluded from this analysis to avoid the potential effect of consecutive escapes on locomotion modes. The explanatory variables were air temperature, relative humidity, grass height (high = 0, low = 1), body length, body weight, and wing length. The correlation between body length, body weight, and wing length was not very strong in both sexes (Table 1). In addition to these explanatory variables, models with a quadratic term for either air temperature or relative humidity were analyzed. However, no significant quadratic effects were detected for temperature (male: $t = -1.518$, $df = 140$, $p = 0.131$; female: $t = -0.623$, $df = 123$, $p = 0.535$) and humidity (male: $t = -0.290$, $df = 140$, $p = 0.772$; female: $t = 0.426$, $df = 123$, $p = 0.671$). Therefore, we proceeded with the model excluding quadratic terms. We also performed a GLM containing an estimate of wing-loading, calculated as body weight divided by the square of wing length, instead of the raw terms of body weight and wing length.

We developed a statistical model to analyze the relationship between locomotion modes during two consecutive escape attempts. The model assumes that each grasshopper escapes by x in the previous escape attempt and y in the next escape attempt with a probability of θ_{xy}, where x and y represent either flying (F) or jumping (J), respectively. The number of grasshoppers in the population that escaped using x in the previous attempt and y in the next attempt was represented by n_{xy}. When an individual selects locomotion modes in two consecutive escapes with probabilities of $\{\theta_{FF}, \theta_{FJ}, \theta_{JF}, \theta_{JJ}\}$, the probability that the set of the numbers of individuals becomes $\{n_{FF}, n_{FJ}, n_{JF}, n_{JJ}\}$ follows the multinomial distribution shown below:

Table 1. Pearson correlation coefficients between body length, body weight, and wing length in females and males.

Sex	Body length vs Body weight	Body length vs Wing length	Body weight vs Wing length
Female	0.848	0.652	0.722
Male	0.736	0.575	0.735

$$P_{(n_{FF},n_{FJ},n_{JF},n_{JJ}|\theta_{FF},\theta_{FJ},\theta_{JF},\theta_{JJ})} = \frac{(n_{FF}+n_{FJ}+n_{JF}+n_{JJ})!}{n_{FF}!n_{FJ}!n_{JF}!n_{JJ}!}(\theta_{FF})^{n_{FF}}(\theta_{FJ})^{n_{FJ}}(\theta_{JF})^{n_{JF}}(\theta_{JJ})^{n_{JJ}}$$

The probability that a grasshopper selects any two consecutive locomotion modes (θ_{xy}) can be represented using the probabilities of flying and jumping determined independently for each escape attempt (here termed "baseline probabilities") and the degree of dependence of the next escape on the previous one. The probability of selecting a locomotion mode in the previous escape is given solely by the baseline probabilities, denoted as ϕ_{Prev} for flying and $1 - \phi_{\text{Prev}}$ for jumping ($0 \le \phi_{\text{Prev}} \le 1$). In contrast, the probability of selecting a locomotion mode in the next escape depends not only on the baseline probabilities, denoted as ϕ_{Next} for flying and $1 - \phi_{\text{Next}}$ for jumping ($0 \le \phi_{\text{Next}} \le 1$) but also on the degree of dependence on the previous escape, denoted as δ. The parameter δ functions similarly to the number of balls added to an urn after picking up the same color balls in Pólya's urn scheme in statistics (Johnson and Kotz 1977). Thus, the probability of selecting a locomotion mode in the next escape is given by $(\alpha + \delta)/(1 + \delta)$ when the same locomotion mode was used previously and $\alpha / (1 + \delta)$ when a different one was used previously, where α denotes the baseline probability of the locomotion mode used in the next escape (i.e., α is either ϕ_{Next} or $1 - \phi_{\text{Next}}$). These expressions show that δ becomes zero when the locomotion modes in the previous and next escape attempts are selected independently. The probabilities of selecting each combination of locomotion modes in two consecutive escape attempts are as follows: $\theta_{\text{FF}} = \phi_{\text{Prev}} (\phi_{\text{Next}} + \delta) / (1 + \delta)$, $\theta_{\text{FJ}} = \phi_{\text{Prev}} (1 - \phi_{\text{Next}}) / (1 + \delta)$, $\theta_{\text{JF}} = (1 - \phi_{\text{Prev}}) \phi_{\text{Next}} / (1 + \delta)$, and $\theta_{\text{JJ}} = (1 - \phi_{\text{Prev}}) (1 - \phi_{\text{Next}} + \delta) / (1 + \delta)$.

The maximum likelihood estimation was used to fit the statistical model to data from the first and second escapes, as well as from the second and third escapes, segmented by sex and grass height. Our statistical model examined two hypotheses regarding locomotion modes during two consecutive escape attempts. First, we tested whether the locomotion modes in consecutive escape attempts were selected independently (i.e., $\delta = 0$). Second, we examined whether grasshoppers used each locomotion mode with the same probability in both the previous and next escape attempts (i.e., $\phi_{\text{Prev}} = \phi_{\text{Next}}$). These hypotheses were evaluated using likelihood ratio tests (Lewis et al. 2011).

All the statistical analyses utilized R 4.2.2 (R Core Team 2022) in R Studio 2022.12.0.353 (Posit team 2022). The Brunner–Munzel test was conducted using the "brunnermunzel" package (Ara 2020). The significance level was set at 0.05. Maxima 5.38.1 (Maxima 2016) along with wxMaxima 16.4.2 was used to analyze the statistical models.

Results

Data were collected from 131 females and 148 males. Of these, data from 52 females and 63 males were obtained from the high-grass site, while data from 79 females and 85 males were obtained from the low-grass sites.

Locomotion modes were related to sex and DF in all three escape attempts. Females escaped by jumping more frequently than males at both the high-grass (Fig. 2A) and low-grass (Fig. 2B) sites (Fisher's exact test: $p = 0.016$ for the first escape at the high-grass site; $p < 0.001$ in all other cases). Females that escaped by flying exhibited longer DFs than those that escaped by jumping at both the high-grass (Fig. 3A) and low-grass sites (Fig. 3B). The same was true for males at both the high-grass (Fig. 3C) and low-grass sites (Fig. 3D).

The FIDs of grasshoppers that escaped by flying differed from those that escaped by jumping, depending on sex, grass height, and number of consecutive escape attempts (Fig. 4). In the first escape, FIDs did not differ significantly between grasshoppers that flew and those that jumped, regardless of sex or grass height. In the second escape, females that jumped at the low-grass sites had shorter FIDs than those that flew at the same sites (Fig. 4B). Females at the high-grass site and males at both the high- and low-grass sites showed no significant differences in their second FIDs between locomotion modes. In the third escape, females at both the high- and low-grass sites (Fig. 4A, B) and males at the low-grass sites (Fig. 4D) showed shorter FIDs in individuals that jumped than in those that flew. Males at the high-grass site showed no significant differences in their third FIDs between flying and jumping.

Locomotion modes in the first escape were related to air temperature and humidity in both sexes and wing length in females (Table 2). Both females and males escaped by flying more frequently as air temperature increased, while flying frequency decreased with rising humidity. Females with longer wings escaped by flying more frequently than those with shorter wings. Similar results were contained in the model with the estimate of wing-loading: The estimate was not significantly related to locomotion modes in males ($t = 1.463$, $df = 142$, $p = 0.146$), whereas females with larger estimates of wing-loadings escaped by jumping more frequently ($t = 2.090$, $df = 125$, $p = 0.039$).

During repeated escape attempts, *O. yezoensis* preferred the locomotion mode used in previous escapes (Table 3). Grasshoppers more frequently selected the same locomotion mode as in the previous escape attempt than would be expected from independent decisions on locomotion modes in any two consecutive attempts except for the second and third escapes of females at the high-grass site. For the third escape attempt of females at the high-grass site, the degree of dependence on the second escape was not significant, although it did have a positive value, similar to other cases.

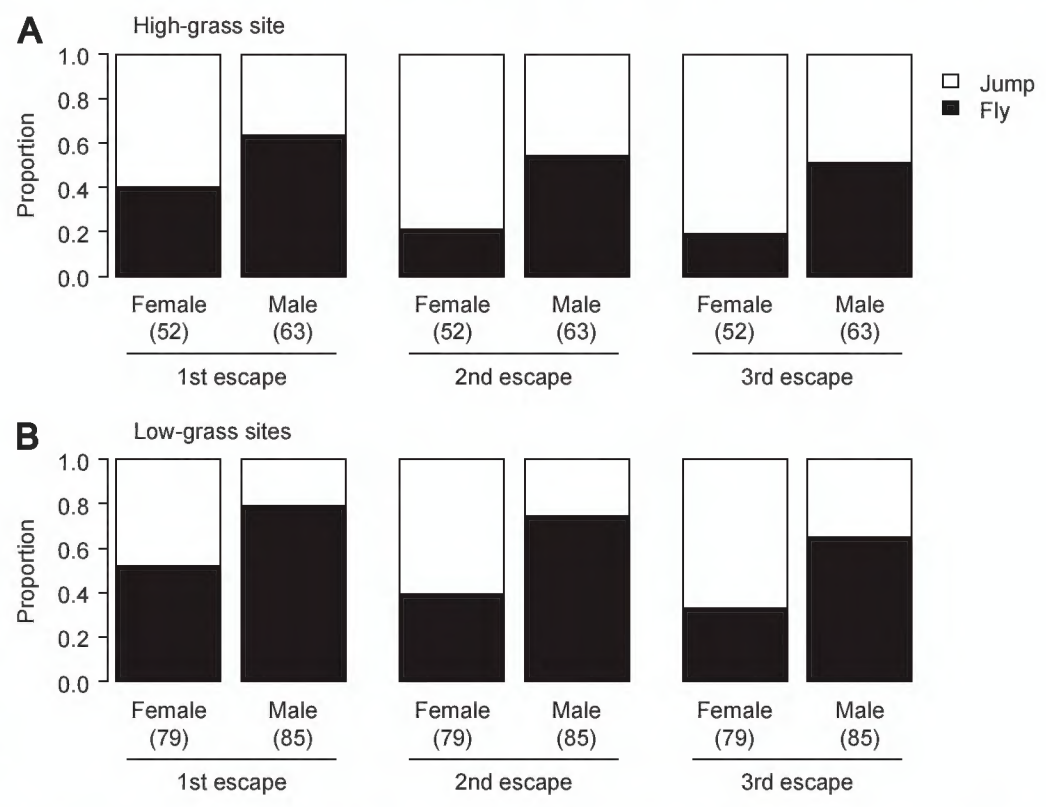

Fig. 2. Proportion of jumping and flying used by *O. yezoensis* during three consecutive escape attempts. **A.** Escape attempts at the high-grass site; **B.** Escape attempts at low-grass sites. The number of individuals is shown in parentheses.

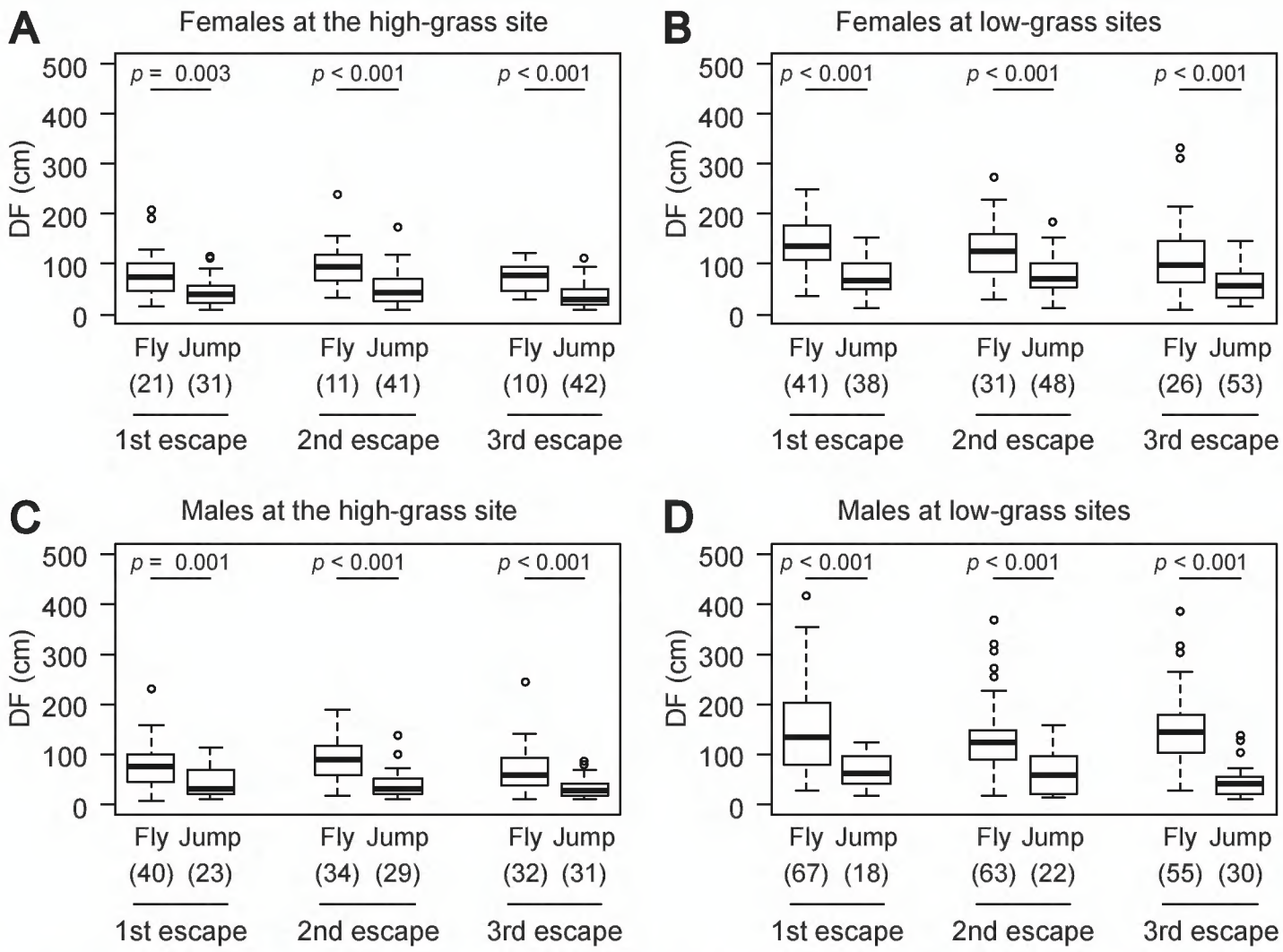

Fig. 3. Relationships between locomotion modes and DF. **A.** Females at the high-grass site; **B.** Females at low-grass sites; **C.** Males at the high-grass site; **D.** Males at low-grass sites. The centerline, lower edge, and upper edge of each box represent the median, first quantile, and third quantile, respectively. The lower whisker shows the minimum value not smaller than the first quantile minus 1.5 times the interquartile range, while the upper whisker shows the maximum value not larger than the third quantile plus 1.5 times the interquartile range. Data points outside the box-and-whisker plots are shown as open circles. The number of individuals is shown in parentheses. *P*-values from the Brunner–Munzel tests are displayed when they are less than 0.05.

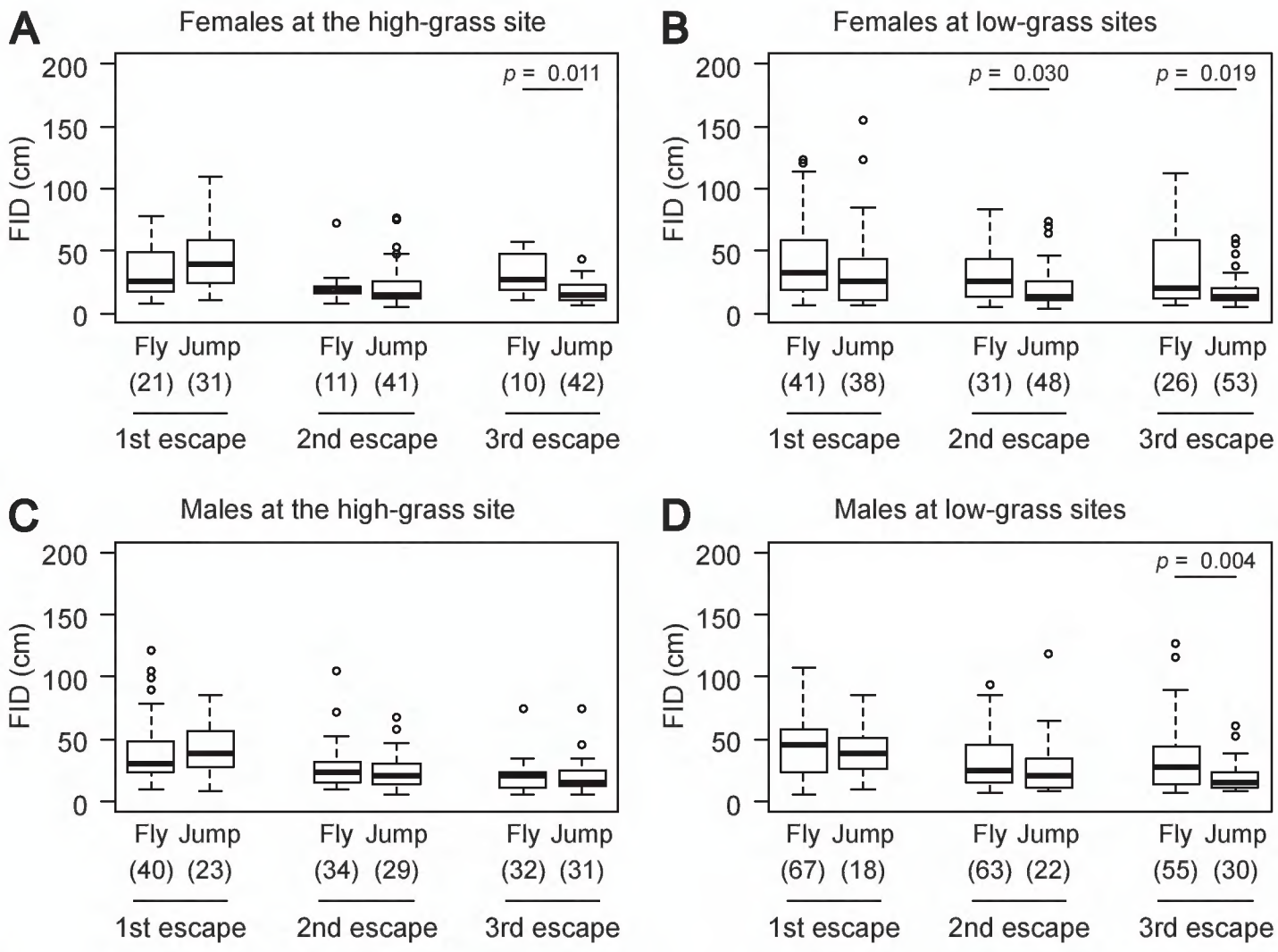

Fig. 4. Relationships between locomotion modes and FID. **A.** Females at the high-grass site; **B.** Females at low-grass sites; **C.** Males at the high-grass site; **D.** Males at low-grass sites. The centerline, lower edge, and upper edge of the box represent the median, first quantile, and third quantile, respectively. The lower whisker shows the minimum value not smaller than the first quantile minus 1.5 times the interquartile range, while the upper whisker shows the maximum value not larger than the third quantile plus 1.5 times the interquartile range. Data points outside the box-and-whisker plots are shown as open circles. The number of individuals is shown in parentheses. *P*-values from the Brunner–Munzel tests are displayed when they are less than 0.05.

Table 2. Results of GLMs on locomotion modes in the first escape attempt. A quasibinomial error structure in glm function of R and logit link were used. All the explanatory variables were included in the model. Degrees of freedom were 124 for females and 141 for males.

Sex	Explanatory variable	Coefficient	SE	*t*	*p*
Female	(Intercept)	11.205	4.505	2.487	0.014
	Grass height	-0.439	0.428	-1.026	0.307
	Temperature	-0.333	0.100	-3.322	0.001
	Humidity	0.066	0.024	2.781	0.006
	Body length	-0.153	0.169	-0.903	0.368
	Wing length	-0.355	0.154	-2.307	0.023
	Body weight	4.691	2.919	1.607	0.111
Male	(Intercept)	5.332	4.971	1.073	0.285
	Grass height	-0.667	0.487	-1.371	0.173
	Temperature	-0.298	0.101	-2.960	0.004
	Humidity	0.071	0.026	2.716	0.007
	Body length	0.020	0.238	0.082	0.935
	Wing length	-0.303	0.205	-1.479	0.141
	Body weight	0.958	8.200	0.117	0.907

Females at both the high- and low-grass sites exhibited a lower baseline probability of flying during the second escape compared to the first. In other cases, the baseline probabilities of flying did not differ significantly across consecutive escapes.

Discussion

The locomotion modes of *O. yezoensis* were influenced by prey traits such as sex and wing length, environmental factors including ambient temperature and relative humidity, and the predator trait of persistence in approach. Locomotion modes were also associated with two other escape strategies: DF and FID. We note that data were not collected from individuals whose escape performance was so high that a human investigator lost sight of their escape. Therefore, our data have the potential for bias toward individuals with low escape performance. This common problem of using a human investigator as a predator model should be tackled in future studies.

Females exhibited a greater tendency to use jumping as a locomotion mode for escape than males. This sex-specific difference in locomotion mode has also been observed in other grasshopper species. For instance, in *Phymateus morbillosus* (Linnaeus, 1758), males consistently utilize flight, while females exclusively employ jumping during escape (Gäde 2002). Similarly, while both sexes of *Acrida cinerea* (Thunberg, 1815) use both flying and jumping for escape, males exhibit a higher flying frequency than females (Kuga and Kasuya 2024). These observations align with the established trade-off between flight and fecundity in grasshoppers, with females investing more in reproduction than males (Chang et al. 2021). This flight-reproduction trade-off may increase the frequency of jumping in female *O. yezoensis*. Females are larger and heavier than males (body length: Mean ± SD = 32.707 ± 2.340 mm, n = 131 vs 26.697 ± 1.589 mm, n = 148; body weight: Mean ± SD = 0.806 ± 0.150 g vs 0.404 ± 0.055 g, n = 148), and thus the larger wing-loadings of the females may deter flying. Identifying factors causing the sex difference in locomotion modes during escape is a future problem.

Grasshoppers that escaped by flying had longer DFs than those that escaped by jumping, regardless of sex, grass height, or number of consecutive escape attempts. This pattern of individuals utilizing flight achieving longer DFs than those utilizing jumping has also been observed in the pygmy grasshopper *Tetrix subulata* (Linnaeus, 1758) (Forsman 1999). Flying is a locomotion mode that allows grasshoppers to escape over greater distances. However, a small subset of individuals that jumped did manage to escape farther than those that flew (Fig. 3), indicating that locomotion mode is not the sole determinant of DFs.

Interestingly, FIDs in *O. yezoensis* were occasionally shorter in individuals that jumped than those that flew. For cryptic prey species, hiding rather than escaping becomes an effective antipredation strategy, especially if the predator has not yet detected the prey (Broom and Ruxton 2005). Therefore, a grasshopper that cannot escape farther by flying may delay the initiation of escape and adopt a hiding strategy instead. Significant differences in FIDs between individuals that jumped and those that flew were observed under specific conditions related to the number of repeated escape attempts, grass height, and sex. The FIDs of prey animals are influenced by a multitude of factors (Stankowich and Blumstein 2005), and the relationship between FID and locomotion mode is likely to vary depending on these factors.

The locomotion mode in the first escape attempt was related to ambient temperature and relative humidity in both males and females and to wing length in females. High ambient temperatures increased the flying frequency of *O. yezoensis*, similar to patterns observed in locusts (Maeno et al. 2019) and pygmy grasshoppers (Forsman 1999). Conversely, escape by jumping increased with high relative humidity. This observation aligns with findings in some bee and wasp species, where high humidity decreases wingbeat frequency (Parmezan et al. 2021). Under high-humidity conditions, *O. yezoensis* may experience reduced wingbeat frequency, hindering effective flight. Furthermore, female *O. yezoensis* with longer wings and thus lower wing-loadings

Table 3. Estimates and results of likelihood ratio tests for statistical models analyzing two consecutive locomotion modes. Definition: NH, null hypothesis of the likelihood ratio test.

Sex	Grass height	Order of attempt	n	Estimates			NH: $\Phi_1 = \Phi_2$			NH: $\delta = 0$		
				Φ_1	Φ_2	δ	χ^2	*df*	*p*	χ^2	*df*	*p*
Female	High	1st to 2nd	52	0.404	0.135	0.397	6.738	1	0.009	6.040	1	0.014
		2nd to 3rd	52	0.212	0.187	0.278	0.077	1	0.781	2.355	1	0.125
	Low	1st to 2nd	79	0.519	0.236	1.239	5.884	1	0.015	27.612	1	<0.001
		2nd to 3rd	79	0.392	0.244	1.343	1.699	1	0.192	29.038	1	<0.001
Male	High	1st to 2nd	63	0.635	0.465	0.783	2.039	1	0.153	11.668	1	<0.001
		2nd to 3rd	63	0.540	0.484	0.754	0.223	1	0.637	11.964	1	<0.001
	Low	1st to 2nd	85	0.788	0.691	1.072	1.011	1	0.315	17.826	1	<0.001
		2nd to 3rd	85	0.741	0.551	1.020	3.291	1	0.070	17.847	1	<0.001

escaped by flying more frequently. This observation is consistent with the trade-off between wing-size and reproduction reported in the pygmy grasshopper *T. subulata* (Steenman et al. 2015). Female *O. yezoensis* with longer wings may invest more in flight, whereas those with short wings may invest in fecundity and consequently opt to escape by jumping.

The baseline probability of flying, which enables a longer DF, remained relatively stable across escape attempts, except during females' first and second escapes. This contrasts with the variability of DFs observed in response to repeated approaches in other grasshopper species. For instance, *Dissosteira carolina* (Linnaeus, 1758) (Cooper 2006) and *Schistocerca alutacea* (Harris, 1841) (Bateman and Fleming 2014) increase DFs in response to persistent approaches, while *Psinidia fenestralis* (Serville, 1838) exhibits a decrease in DF (Bateman and Fleming 2014), and *Chortophaga australior* Rehn & Hebard, 1911 displays a slow oscillation in DF (Collier and Hodgson 2017). In our study, female *O. yezoensis* showed a decreased baseline probability of flying through the first and second escapes. This decrease may be attributed to the reduced energy reserves available for flight.

In most cases, the grasshopper repeated the same locomotion mode during consecutive escape attempts more frequently than expected from an independent selection of locomotion modes. Three non-mutually exclusive hypotheses can explain the repeated use of the same locomotion mode. First, the previous locomotion mode allowed the grasshopper to escape successfully and thus may have been used again in subsequent predatory attacks. In this scenario, we predict that a grasshopper will change its locomotion mode if injured during the previous predatory encounter.

Second, physiological constraints may cause grasshoppers to repeat the same mode of locomotion. Flying and jumping of grasshoppers differ in the underlying neural and metabolic pathways involved (Burrows 1996, Pflüger and Duch 2011). If transitioning between the two locomotion modes requires more time for preparation before escaping than repeating the same locomotion mode, repeated use of the same locomotion mode would be expected.

Third, frequent repetition of the same locomotion mode may occur due to individual differences in the escape decisions. Many prey animals exhibit individual differences in escape behaviors, such as hiding time in a refuge and flight initiation distance (López and Martín 2015). If the probability of selecting a locomotion mode for escape differs between individuals, the effect of previous escapes on subsequent ones will be detected by analyses that assume no individual differences in the population (see Suppl. material 1). This phenomenon is similar to the Wahlund effect in population genetics (Hartl and Clark 2007) or Simpson's paradox in statistics (Agresti 2013). To examine the effect of individual differences, data should be collected from individuals under various conditions. Research on locomotion mode selection during repeated escape attempts is still insufficient. The statistical models developed in this study and future adaptation thereof will benefit future research on repeated escape behavior in prey animals.

This study revealed factors related to locomotion modes during escape in *O. yezoensis*, including sex, wing length, ambient temperature, relative humidity, FID, DF, and consecutive approaches. Grasshoppers are commonly used in studies of escape behavior; however, while most research has focused on FID or DF rather than locomotion modes, our findings revealed that the locomotion modes in *O. yezoensis* are associated with both FID and DF. These results highlight the importance of considering locomotion modes when studying FID or DF in grasshoppers.

Acknowledgements

We acknowledge the members of the Laboratory of Ecological Science at Kyushu University for their kind advice on our study. We appreciate Kyushu University allowing the field experiment in its conservation area. We would like to thank Editage (https://www.editage.jp) for English language editing. We are grateful to Dr. Eric Butler and Dr. Diptarup Nandi for their valuable comments during the review process.

References

Agresti A (2013) Categorical Data Analysis. 3rd ed. John Wiley & Sons, Hoboken, New Jersey, 752 pp.

Ara T (2020) "brunnermunzel": (Permuted) Brunner-Munzel Test. https://doi.org/10.32614/CRAN.package.brunnermunzel

Bateman PW, Fleming PA (2014) Switching to plan B: Changes in the escape tactics of two grasshopper species (Acrididae: Orthoptera) in response to repeated predatory approaches. Behavioral Ecology and Sociobiology 68: 457–465. https://doi.org/10.1007/s00265-013-1660-0

Bateman PW, Fleming PA (2015) Invertebrates. In: Cooper Jr WE, Blumstein DT (Eds) Escaping From Predators: An Integrative View of Escape Decisions. Cambridge University Press, Cambridge, 177–196. https://doi.org/10.1017/CBO9781107447189.008

Belton P (1986) Sounds of insects in flight. In: Danthanarayana W (Ed.) Insect Flight: Dispersal and Migration. Springer-Verlag, Berlin, Germany, 60–70. https://doi.org/10.1007/978-3-642-71155-8_5

Broom M, Ruxton GD (2005) You can run—or you can hide: Optimal strategies for cryptic prey against pursuit predators. Behavioral Ecology 16: 534–540. https://doi.org/10.1093/beheco/ari024

Burrows M (1996) The Neurobiology of an Insect Brain. Oxford University Press, New York. https://doi.org/10.1093/acprof:oso/9780198523444.001.0001

Butler EM (2013) Species-specific escape behaviour in grasshoppers. Behaviour 150: 1531–1552. https://doi.org/10.1163/1568539X-00003108

Chang H, Guo X, Guo S, Yang N, Huang Y (2021) Trade-off between flight capability and reproduction in Acridoidea (Insecta: Orthoptera). Ecology and Evolution 11: 16849–16861. https://doi.org/10.1002/ece3.8317

Collier A, Hodgson JYS (2017) A shift in escape strategy by grasshopper prey in response to repeated pursuit. Southeastern Naturalist 16: 503–515. https://doi.org/10.1656/058.016.0403

Cooper Jr WE (2006) Risk factors and escape strategy in the grasshopper *Dissosteira carolina*. Behaviour 143: 1201–1218. https://doi.org/10.1163/156853906778691595

Cooper Jr WE, Blumstein DT (2015) Escaping From Predators: An Integrative View of Escape Decisions. Cambridge University Press, Cambridge, 442 pp. https://doi.org/10.1017/CBO9781107447189

Dangles O, Pierre D, Christides JP, Casas J (2007) Escape performance decreases during ontogeny in wild crickets. Journal of Experimental Biology 210: 3165–3170. https://doi.org/10.1242/jeb.004648

de Barros FC, de Carvalho JE, Abe AS, Kohlsdorf T (2010) Fight versus flight: The interaction of temperature and body size determines antipredator behaviour in tegu lizards. Animal Behaviour 79: 83–88. https://doi.org/10.1016/j.anbehav.2009.10.006

Forsman A (1999) Temperature influence on escape behaviour in two species of pygmy grasshoppers. Écoscience 6: 35–40. https://doi.org/10.1080/11956860.1999.11952202

Gäde G (2002) Sexual dimorphism in the pyrgomorphid grasshopper *Phymateus morbillosus*: From wing morphometry and flight behaviour to flight physiology and endocrinology. Physiological Entomology 27: 51–57. https://doi.org/10.1046/j.1365-3032.2002.00268.x

Harris TW (1841) A Report on the Insects of Massachusetts, Injurious to Vegetation. Folsom, Wells, and Thurston, Cambridge, 459 pp. https://doi.org/10.5962/bhl.title.6091

Hartl DL, Clark AG (2007) Principles of Population Genetics. 4th ed. Sinauer Associates, Sunderland, 672 pp.

Hochkirch A, Zimmermann M, Keithahn C, Länder S, Peiter A, Folger-Rüter M, Harmuth C, Vogt S, Zimmermann M, Hellwig F, Gulau A, Mühl H (2002) A field study of the escape behaviour of *Tetrix subulata* (Linnaeus, 1758) and *Tetrix tenuicornis* (Sahlberg, 1893) (Orthoptera: Tetrigidae). Articulata 17: 19–31.

Johnson NL, Kotz S (1977) Urn Models and Their Application: An Approach to Modern Discrete Probability Theory. Wiley, New York, 402 pp.

Kuga T, Kasuya E (2024) Factors related to sound production by the Chinese grasshopper *Acrida cinerea* during escape. Journal of Orthoptera Research 33: 13–19. https://doi.org/10.3897/jor.33.100865

Lagos PA (2017) A review of escape behaviour in orthopterans. Journal of Zoology 303: 165–177. https://doi.org/10.1111/jzo.12496

Lee S-i, Hwang S, Joe Y-e, Cha H-k, Joo G-h, Lee H-j, Kim J-w, Jablonski PG (2013) Direct look from a predator shortens the risk-assessment time by prey. PLOS ONE 8: e64977. https://doi.org/10.1371/journal.pone.0064977

Lewis F, Butler A, Gilbert L (2011) A unified approach to model selection using the likelihood ratio test. Methods in Ecology and Evolution 2: 155–162. https://doi.org/10.1111/j.2041-210X.2010.00063.x

Linnaeus C (1758) Systema Naturae per Regna tria Naturae, secundum Classes, Ordines, Genera, Species, cum Characteribus, Differentiis, Synonymis, Locis. 10th ed. Laurentii Salvii, Holmiae, 824 pp. https://doi.org/10.5962/bhl.title.542

López P, Martín J (2015) The personality of escape. In: Cooper Jr WE, Blumstein DT (Eds) Escaping From Predators: An Integrative View of Escape Decisions. Cambridge University Press, Cambridge, 385–404. https://doi.org/10.1017/CBO9781107447189.016

Maeno KO, Ould Ely S, Ould Mohamed S, Jaavar MEH, Nakamura S, Ould Babah Ebbe MA (2019) Defence tactics cycle with diel microhabitat choice and body temperature in the desert locust, *Schistocerca gregaria*. Ethology 125: 250–261. https://doi.org/10.1111/eth.12845

Maxima (2016) Maxima, a Computer Algebra System. Version 5.38.1. http://maxima.sourceforge.net/

Miller BM, McDonnell LH, Sanders DJ, Lewtas KLM, Turgeon K, Kramer DL (2011) Locomotor compensation in the sea: Body size affects escape gait in parrotfish. Animal Behaviour 82: 1109–1116. https://doi.org/10.1016/j.anbehav.2011.08.005

Mitsuhashi J (2012) Entomophagy of all times and places. Ohmsha, Tokyo, 290 pp. [in Japanese]

Nonaka K (2009) Feasting on insects. Entomological Research 39: 304–312. https://doi.org/10.1111/j.1748-5967.2009.00240.x

Parmezan ARS, Souza VMA, Žliobaitė I, Batista GEAPA (2021) Changes in the wing-beat frequency of bees and wasps depending on environmental conditions: A study with optical sensors. Apidologie 52: 731–748. https://doi.org/10.1007/s13592-021-00860-y

Pflüger H-J, Duch C (2011) Dynamic neural control of insect muscle metabolism related to motor behavior. Physiology 26: 293–303. https://doi.org/10.1152/physiol.00002.2011

Posit team (2022) RStudio: Integrated Development Environment for R. http://www.posit.co/

R Core Team (2022) R: A Language and Environment for Statistical Computing. https://www.R-project.org/

Rehn JAG, Hebard M (1911) Records of Georgia and Florida Orthoptera, with the descriptions of one new species and one new subspecies. Proceedings of the Academy of Natural Sciences of Philadelphia 62: 585–598. https://www.jstor.org/stable/4063334

Rodriguez-Prieto I, Fernández-Juricic E, Martín J (2008) To run or to fly: Low cost versus low risk escape strategies in blackbirds. Behaviour 145: 1125–1138. https://doi.org/10.1163/156853908784474489

Serville JGA (1838) Histoire naturelle des insectes. Orthoptères. Librairie Encylopédique de Roret, Paris, [i–xviii,] 776 pp. [pl. 1–14] https://doi.org/10.5962/bhl.title.16081

Shiraki T (1910) Acrididen Japans. Fukuin printing co., ltd., Yokohama, 90 pp. http://archive.org/details/acrididenjapans00shirrich [January 6, 2025]

Stankowich T, Blumstein DT (2005) Fear in animals: A meta-analysis and review of risk assessment. Proceedings of the Royal Society B: Biological Sciences 272: 2627–2634. https://doi.org/10.1098/rspb.2005.3251

Steenman A, Lehmann AW, Lehmann GUC (2015) Life-history trade-off between macroptery and reproduction in the wing-dimorphic pygmy grasshopper *Tetrix subulata* (Orthoptera Tetrigidae). Ethology Ecology & Evolution 27: 93–100. https://doi.org/10.1080/03949370.2014.885466

Thunberg CP (1815) Hemipterorum maxillosorum genera illustrata plurimisque novis speciebus ditata ac descripta. Mémoires de l'Académie Impériale des Sciences de St. Pétersbourg 5: 211–301.

Whitman DW, Vincent S (2008) Large size as an antipredator defense in an insect. Journal of Orthoptera Research 17: 353–371. https://doi.org/10.1665/1082-6467-17.2.353

Supplementary material 1

Author: Tatsuru Kuga, Eiiti Kasuya
Data type: pdf
Explanation note: Potential bias in estimating the degree of dependence on previous escape attempts caused by the existence of subpopulations.
Copyright notice: This dataset is made available under the Open Database License (http://opendatacommons.org/licenses/odbl/1.0/). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.
Link: https://doi.org/10.3897/jor.35.146467.suppl1